A New Species of *Harpa* (Gastropoda: Volutoidea) from the Neogene of the Dominican Republic: Paleobiogeographical Implications

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Abstract. A new species of Harpa, H. daisyae is described from the Upper Miocene Cercado Formation of the Dominican Republic. The genus in the tropical American Neogene is discussed, phylogenetic groups within the genus are suggested, and paleobiogeographic implications commented.

INTRODUCTION

The rich and diverse Neogene assemblages from the northern Dominican Republic have been known for >150 yr (Sowerby, 1850). More recently, these assemblages have been studied in a systematic way as part of the "Dominican project," and these results published in a series of papers that appeared in Bulletins of American Paleontology (Vokes, 1989, 1998; Jung & Petit, 1990; Jung, 1994; Freiheit & Greary, 2009). For an account of the history and methodology of the various Dominican collecting ventures, see Vokes (1989).

This paper is the first of a series of papers describing new gastropod taxa from these Dominican assemblages belonging to taxonomic groups already monographed by the Dominican project but discovered subsequent to the publication of these works. These new taxa also represent the result of 20 yr collecting in the Dominican Republic by one of us (B.L.).

The genus *Harpa* in the Dominican Neogene was revised by Vokes in 1998. The presence of fossils belonging to the genus *Harpa* in the Dominican Republic Neogene was first noted by Gabb (1873); the specimens were later described by Pilsbry (1922) as *Harpa americana*. This species is represented by two specimens from an unnamed unit in the López section of the Yaque del Norte River, ascribed to the same age of the Cercado Formation, Upper Miocene by Vokes

(1998). We here describe a second Harpa species cooccurring in these deposits. It is also from the López section, from sandy unit close to the river bed toward the east bank and probably is also of the same age as the Cercado Formation (Vokes, personal communication). The bed of the Yaque del Norte River is very dynamic and the units exposed change accordingly. Conglomerates, coarse-to-fine sands, and clays are exposed at different sections of the river bed when the river is at its lowest, and the specimen described here was found in a bed composed of fine yellow sands situated approximately 2.9-3 km upstream of the mouth of Angostura Gorge (Figure 1), Rio Yaque del Norte, with sparsely scattered fossils of molluscs, mostly Vokesimurex messorius (Sowerby, 1841), and a few other molluscs, none of which were stratigraphic index taxa.

For a more detailed geological and stratigraphic setting and geographic location of the study, see Saunders et al. (1986;23–30).

MATERIALS AND METHODS

The material described here is from the Bernard Landau collection, which will be housed in the Naturhistorisches Museum Wien (NHMW collection [coll.]), Vienna, Austria. Type material is deposited in the Naturhistorisches Museum Wien (NHMW coll.), Vienna, Austria.

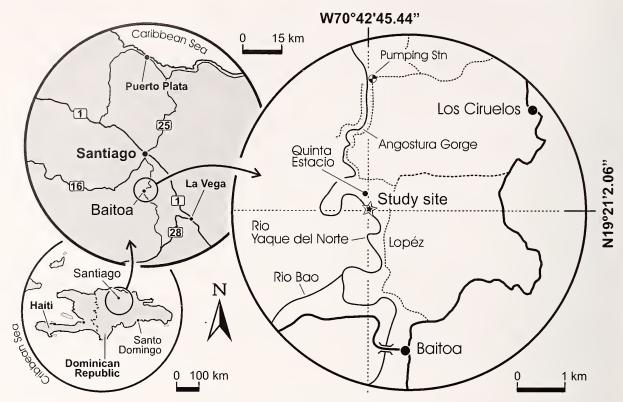


Figure 1. Geographic location of study area.

SYSTEMATIC PALAEONTOLOGY VOLUTOIDEA

Harpinae Bronn, 1849 Harpinae Bronn, 1849 *Harpa* Röding, 1798 *Harpa daisyae* nov. sp. (Figures 2–5)

Type material and dimensions: Holotype; NHMW 2009z0076/0001, height 22.5 mm.

Etymology: Small and pretty, like my daughter Daisy (B.L.).

Type locality: Lopez section, Rio Yaque del Norte, upstream of the mouth of Angostura Gorge, Dominican Republic (Saunders et al., 1986;fig. 23; and Figure 1).

Type stratum: Unnamed unit of the same age of the Cercado Formation (Upper Miocene).

Diagnosis: A small-shelled *Harpa*, with a multispiral protoconch of smooth rounded whorls, and a low spired teleoconch with, an elongated last whorl, very

narrow and relatively close-set axial ribs, weak spiral sculpture of roughly equal strength to the axial growth lines giving the shell surface a finely reticulate pattern, outer lip smooth, without barbs.

Description: Shell very small for genus, ovate; spire low, depressed, rapidly increasing in size; last whorl and aperture very large. Protoconch poorly preserved with nucleus missing, multispiral, high dome-shaped, tilted slightly at an angle to the main axis of the shell, composed of at least three smooth whorls. Last protoconch whorl inflated, bearing three strongly prosocline riblets toward the protoconch-teleoconch boundary, which is sharply delimited by a sinusoid scar. Teleoconch consists of three whorls with a narrow, almost horizontal subsutural platform, broadly rounded below with the periphery at the adapical suture. Axial ornament strongly predominant, consisting of 11 very narrow elevated ribs, opistocyrt on the first teleoconch whorl, straight below, 13 on the last whorl. The ribs are reflected abaxially at the shoulder, fuse with the adapical portion of the preceding whorl to cover the adapical suture entirely. A small auricle develops on the axial ribs at the shoulder on the second half of the penultimate whorl and last whorl. Spiral sculpture consists of very weak, narrow, irregular cords cut by close-set axial growth lines giving the surface a finely reticulate pattern. Last whorl very large, 90% of

total height, barrel-shaped. Aperture large, 78% total height, elongate. Outer lip slightly thickened by labral varix, weakly flared abapically, not barbed on the edge, smooth within; anal canal relatively wide, rounded, shallow; siphonal canal open, short, slightly recurved. Parietal callus expanded, closely adherent, thin, clearly delimited; columellar callus slightly thicker, somewhat detached over the siphonal fasciole. Siphonal fasciole broad, rounded, with the axial sculpture deflected onto it as elevated scales.

Comparison: Harpa daisyae nov. sp. is the smallest adult Harpa shell known from the Tropical American Neogene. It is most similar in size and shape to the Recent Harpa gracilis Broderip, W. J. & G. B. I Sowerby, 1829 (Figures 6, 7) that is mainly a Polynesian species but that also occurs at Clipperton Island in the eastern Pacific (Rehder, 1973), but this Harpa has an even more elongated shell, with a higher spire and the outer lip is more flared abapically. Like H. gracilis, it has a smooth outer lip with no barbs. Of the Tropical American species, Harpa istlauica Vokes, 1984 is the most similar (Figures 8-10), but the latter species has a wider, less elongated shell, with more numerous axial ribs that form a small spine at the shoulder rather than a rounded auricle as in H. daisyae. According to the original description, the protoconch of H. isthmica is keeled (Vokes, 1984: 57), whereas that of H. daisyae has uniformly rounded whorls. Harpa myrmia Olsson, 1931 and Harpa crenata Swainson, 1822 (Figures 11, 12) both have much broader shells and more widely spaced axial ribs with spines at the shoulder, and in H. crenata a double set of spines.

GENUS *HARPA* IN THE TROPICAL AMERICAN NEOGENE

The genus *Harpa* in the Tropical American Neogene has attracted a fair amount of attention and was comprehensively covered by Vokes (1984). Five species of *Harpa* Röding, 1798 have been described from the tropical American Neogene, and although fairly widespread in the Tropical American deposits, it is invariably rare in abundance; therefore, new records are worthy of mention to reveal the Neogene history and palaeobiogeography of the genus.

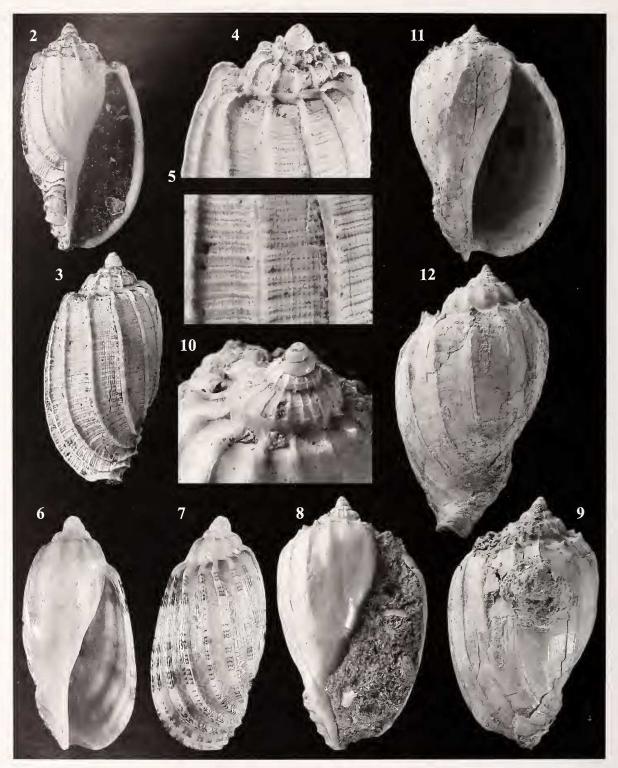
Harpa first appears in the Cenozoic of tropical America in the Lower Oligocene Chira Formation of Peru (Olsson, 1931) represented by Harpa myrmia, characterized by its extremely heavy ribs and broad extension of the axial ribs of the last whorl; these ribs are appressed against the previous whorl and completely cover the suture and most of the penultimate whorl. Chronostratigraphically, the next occurrence is in the Lower Miocene Cantaure Formation of Venezuela. Identified as Harpa myrmia by Gibson-Smith & Gibson-Smith (1982), it also has heavy axial ribs, with

extensions covering the suture. The width of the ribs are somewhat variable (Gibson-Smith & Gibson-Smith (1982: figs. 1, 2), and three further specimens (B.L coll.) have relatively narrower ribs, whereas the shell described in Gibson-Smith & Gibson-Smith (1982; fig. 3) has broad ribs, similar to the Peruvian specimen. As noted by Vokes (1984), more Peruvian material is needed to confirm whether the two specimens are conspecific.

Harpa americana Pilsbry, 1922 from the Cercado Formation, Upper Miocene of the Dominican Republic has a relatively elongated shell, with low, nodular varices and a nonpolished surface. It is known from only two specimens (Vokes, 1998), and our collecting efforts have not brought any more specimens to light. Harpa istlmica Vokes, 1984 from the Agueguexquite Formation, Middle Pliocene of Mexico (Caribbean) has more numerous and heavier ribs, and a smoother surface to the shell. One of us (B.L.) has found a specimen ascribed to Harpa istlmica in the Ground Creek Formation on Bastimentos Island, Bocas del Toro, Panama (Figures 8–10) dated as Plio-Pleistocene Boundary (Coates et al., 2005).

Lastly, the living H. crenata is characterized by having a more inflated last whorl and fewer axial ribs, with secondary nodes anterior to the shoulder that become prominent shoulder spincs, giving a "doubleshouldered" aspect to the shell (Vokes, 1984); and by having barbs on the edge of the outer lip. There are differences also in the protoconch, consisting of 3.5 whorls in H. crenata and H. istlimica and 4.5 whorls in H. americana (although this is somewhat contradictory; the original description gives an "embryonic whorl count of 3.0"; Pilsbry, [1922]: 337), whereas Vokes [1984: 57] states 4.5 whorls). The presence of H. crenata was recorded in the Lower Pliocene Esmeraldas Formation of Ecuador (Pitt, 1981; Vokes, 1984). The specimen illustrated by Vokes (1984: pl. 1, fig. 5) as H. crenata with some hesitation is rather elongated for the species and lacks the "double-shouldered" aspect to the shell. The second specimen illustrated by Pitt (1981: 155: fig. 1) is also atypical for *H. crenata*, and although broader, in our opinion both represent specimens of H. americana. Harpa crenata does, however, occur in the Lower Pliocene Araya Formation of Venezuela on Cubagua Island (Figure 11) and the Araya Peninsula (Figure 12; Landau et al., 2008).

Vokes (1984) suggested a phylogeny in which *H. myrmia* was a distinct lineage on account of having the sutures crossed by extensions of the ribs, not known in any other species. She suggested it derived from the ancestral *Eocithara* line and left no descendants. In the Caribbean, Vokes (1984) suggested that *H. istlmica* was most similar and possibly ancestral to the Recent West African *H. doris* Röding 1798. She suggested that *H. americana* gave rise to *H. crenata*, and its Early



Figures 2–5. Harpa daisyae nov. sp. Holotype; NHMW 2009z0076/0001 (ex. B.L. coll.), height 22.5 mm. Unnamed unit of same age as Cercado Formation (Upper Mioccne), sandy bed just upstream of the mouth of Angostura Gorge, Rio Yaque del Norte, Dominican Republic. Figure 4. Detail of spire and protoconch. Figure 5. Detail of surface sculpture last whorl. Figures 6–7. Harpa gracilis Broderip, W. J. & G. B. I Sowerby, 1829 (coll. G. T. Poppe). Height 22.8 mm. French Polynesia. Tuamotous Archipelago.

Pliocene relative in Ecuador. Although these extensions to the ribs covering the suture are most marked in *H. myrmia*, they are also present to a lesser degree in *H. istlmica* and *H. daisyae*. Based on close similarities in shell morphology between *H. daisyae* and the Recent Indo-Pacific and eastern Pacific *H. gracilis*, it is likely that the two species are phylogenetically related, although we must stress that the fossil record of *Harpa*, especially in the Indo-Pacific, is very incomplete,

The presence of typical *H. crenata* specimens in the Lower Pliocene of Cubagua Island (Araya Formation) of Venezuela complicates the issue. In our opinion, the shells illustrated by and Pitt (1981) and Vokes (1984) from the Esmeraldas Formation of Ecuador are more typical of *H. americana*. It is likely that *H. americana* existed on both the Atlantic and Pacific portions of the Gatunian palaeobiogeographic province. *Harpa crenata* was restricted to the southern part of the province in the Pliocene and at some stage expanded its range to the Pacific side of the palaeobiogeographic province, with its distribution subsequently restricted to the Pacific after the closure of the Central American seaway.

Harpa is important from a palaeobiogeographic angle, because it is a good example of the group Woodring (1966) called paciphiles, i.e., taxa that were present throughout the Gatunian Neogene Province (see Vermeij & Petuch, 1986; Landau et al., 2008), but that suffered a range contraction after the closure of the Central American Seaway and subsequently became restricted to the Pacific side of their original distribution. With the description of H. daisyae nov. sp., we now have Caribbean fossil representatives of both the living eastern Pacific groups of Harpa: H. daisyae in the H. gracilis group, characterized by small, elongated shells with no barbs on the abapical portion of the outer lip; and H. crenata, one of the few living paciphile species (see Landau et al., 2009) in the Caribbean Lower Pliocene, in the *Harpa* group, with barbs on the abapical portion of the outer lip. Harpa is also an example of a typically tropical and subtropical genus that seems to have been widespread in the Neogene Gatunian Province but never extended its range into the neighboring Caloosahatchian Province to the north, despite this province also being tropical to subtropical (see Vermeij & Petuch, 1986; Landau et al., 2008).

From an ecostratigraphic point of view, *Harpa* is also important, because it is one of the few paciphile taxa that survived the first pulse of paciphile Caribbean disappearances at the end of the Early Pliocene, at approximately 3.5 Ma, before the disappearance of paciphiles from the Caribbean near the end of the Early Pleistocene, at approximately 1 Ma (Landau et al., 2009: fig. 2), and thus one of the paciphile taxa characteristic of the ecostratigraphic Gatunian Neogene Paciphile Molluscan Unit 2 of Landau et al. (2009).

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Figures 8–10. *Harpa istlunica* Vokes, 1984. NHMW 2009z0077/0002 (ex. B.L. coll.), Height 35.2 mm. Plio-Pleistocene Boundary, Ground Creek Formation, Bastimentos Island, Bocas del Toro, Panama. Figure 10. Detail of spire and protoconch.

Figure 11. Harpa crenata Swainson, 1822. NHMW 2009z0077/0003 (ex. B.L. coll.), Height 66.2 mm. Early Pliocene, Araya Formation, Cubagua Group, Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela.

Figure 12. Harpa crenata Swainson, 1822. NHMW 2009z0077/0004 (ex. B.L. coll.), Height 61.8 mm. Lower Pliocene, Amina Formation, Cubagua Group, Cerro Barrigón, Araya Peninsula, Sucre State, Venezuela.

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